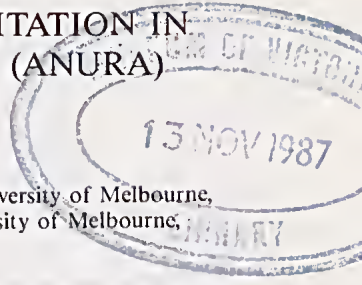


POPULATION ENERGETICS AND FOOD LIMITATION IN TWO SYMPATRIC SPECIES OF *RANIDELLA* (ANURA)

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ABSTRACT: Two species of anuran amphibians, *Ranidella signifera* and *R. parinsignifera*, are broadly sympatric in south-eastern Australia. The energetics of sympatric populations of breeding males were evaluated over four years of study. Although areal population respiration and consumption of food in choruses are as great as in populations of homeothermic vertebrates, the localisation of individuals means that these anuran populations contribute relatively little to energy flow compared with birds or mammals. The ratio of production to respiration in populations of anurans should be intermediate between the analogous ratios in birds and in salamanders. Somatic energy reserves contribute relatively little to energy requirements, so that feeding at breeding sites is essential to finance observed reproductive activity. Standardised measures of reproductive expenditure reveal that males of these species of *Ranidella* expend about as much on annual reproduction as do females of a variety of small reptiles and amphibians. Comparisons of food availability and food requirements indicate that food limitation is likely to occur in sympatric populations of these species of *Ranidella*. Despite this, neither food nor microhabitat segregation occurs.

Humphreys (1979) provided an extensive list of figures for productivity and respiration in populations of animals. He did not refer to studies of population energetics of herpetofaunas, although information does exist (e.g. Alexander & Whitford 1968, Burton & Likens 1975, Nagy & Shoemaker 1975, Bennett & Gorman 1979). Of all of the groups of terrestrial vertebrates, the amphibians have been least studied in terms of population energetics. To my knowledge, the only reference to an aspect of population energetics of anuran amphibians is that of Darevskij and Terentev (1967), but the information presented there is sketchy and indirect. Clearly, an understanding of patterns of energy expenditure and acquisition in terrestrial vertebrates cannot be gained without an empirical basis that spans all groups. For example, Burton and Likens (1975) reported that populations of salamanders have high ratios of production: respiration relative to avian populations in the same forests. They estimated that these caudate amphibians produce five times as much new biomass as do the birds, but engage just one-fifth as much energy flow. Are such patterns characteristic of trends within the terrestrial vertebrates, or are they specific to the species and locations involved? The opportunity to quantify population energetics in amphibians now exists, owing to recent studies of energy budgets of individuals (e.g. Bucher *et al.* 1982, Ryan *et al.* 1983, Mac Nally 1984a, Taigen & Wells 1985). One objective of this paper is to synthesise a diverse range of characteristics of populations of two sympatric species of anuran amphibians (*Ranidella signifera* and *R. parinsignifera*: Leptodaelytidae) so that energy expenditure and acquisition can be evaluated for these species. The information that is used to do so includes data on changes in population density, maintenance metabolism, energy required for reproduction, dynamics of energy stores, and rates of ingestion.

The second part of this study concerns food limitation. Conventional theories of competition and coexis-

tence in guilds assert that morphologically similar, sympatric species should differ along one of three resource dimensions: (1) diet composition; (2) locations of foraging; and/or, (3) times of feeding (Schoener 1974). The idea here is that those phenotypes within populations that specialise in such a way as to overlap relatively little with heterospecifics should accrue significantly more resources, and thereby outcompete other conspecific phenotypes (Schoener 1970, 1974, Pianka 1975, Rosenzweig 1981). That is, the elevated fitness associated with reduced overlap is converted into niche segregation (MacArthur 1972, May & MacArthur 1972). Of course, the resources upon which the "competitive" process depend must be limited relative to the requirements of the putative "competitors". Abrams (1980a, b) suggests that appropriate models of consumer requirements and resource availability might be used to assess limitation. This method is an indirect one in terms of demonstrating true competition [which entails experimental detection of demographic effects (Dunham 1980, Mac Nally 1983b)], but it does have the potential advantage of identifying the resource(s) through which the demographic effects are mediated (Jaeger 1970, 1971). The second objective of this paper, then, is to construct a reasonable model of energy requirements of the two sympatric populations of *Ranidella*, and assess whether food availability is sufficient to cover these requirements without the occurrence of limitation.

NATURAL HISTORY

These species of *Ranidella* are migratory. Breeding individuals of *R. signifera* arrive at ponds in south-central Victoria as early as February, and may continue to breed until December if rainfall is sufficient and consistent enough (Mac Nally 1981b). Individuals of *R. parinsignifera* do not breed until mid-July at the earliest, so that variable amounts of asynchronous breeding occur. Temporal overlap is increased greatly in years in which au-

seasonal (March to May) drought occurs because the breeding activity of *R. signifera* then is concentrated into late winter and spring, when *R. parinsignifera* usually breeds.

This study is concentrated upon the population energetics of breeding males because they are the constituents of anuran populations that are most likely to affect one another (Mac Nally 1979, 1983a). At least in these species of *Ranidella*, breeding males occur in high densities for long periods relative to females (Mac Nally 1979, 1984b). Overall, the figures for components of population energetics are minima because data for females and young are not included. Moreover, the estimates of expenditure and consumption refer to breeding seasons only, which is a common practice in studies of population energetics of migratory species (e.g. Wiens & Nussbaum 1975, Holmes *et al.* 1979).

PROCEDURES

Broadly speaking, there are two main facets to the evaluation of population energetics: (1) expenditure; and, (2) acquisition. Both factors are determined by the spatial densities of males and durations of breeding. Expenditure consists of metabolic requirements incurred during reproductive activity: (1) maintenance metabolism; and, (2) metabolism necessary to accommodate activities such as vocalisations, etc. The energy that is used to finance metabolic expenditure can be derived from two sources: (1) "imported" energy (fat bodies, liver, etc.); and, (2) energy obtained by feeding at breeding locations.

SPATIAL DENSITIES AND DYNAMICS

These variables were determined at Willowmavin site L, 62 km NNW of Melbourne, Victoria (37°17'S, 144°58'E). Chorus dynamics were studied from 1977 to 1980. The measurement procedure was as follows. A permanent reference point was established. For each occasion that information was collected (a chorus "mapping"), a 50 m measuring tape was anchored at the permanent point, and then laid parallel to the long axis of the pond. Vocalising males of both species were located. They were captured by hand, and their positions marked by using numbered stakes. These males were individually marked by toe-clipping (Martof 1953), and then returned to their respective positions. Satellite males were detected by direct visualisation, or by searching the vicinity of stations of calling males. Locations of stakes relative to the permanent point were noted for each mapping. These data provided the basic information concerning the spatial dynamics of breeding males and temporal changes in densities.

EXPENDITURE OF ENERGY

Temperature regime: Metabolic rates of poikilothermic animals depend upon ambient temperature (Prosser 1973; Results). Therefore, it is necessary to establish the thermal regime experienced by the animals to be able to estimate energy expenditure. Two sets of information were used to attempt to do so. First, records of temperature

fluctuations were obtained from the Victorian Bureau of Meteorology for local weather stations. Second, direct measurements of temperature were made at the locations of the animals themselves. These temperatures were recorded during chorus mappings, during the measurement of schedules of vocalisations (see below), and also at all times during the day and night to obtain a fully representative idea of the thermal regime. Although the records derived from the weather stations are included here, one should bear in mind that they are liable to be of less use than direct measurements because they do not take into account the stabilising influence of lentic pools or ponds of water, along whose banks the animals are located. Clearly, the direct measurements should portray a clearer picture in relation to the thermal regime that is experienced by the animals.

Maintenance metabolism: Males of both species of *Ranidella* were collected from a nearby pond, Willowmavin F&M (3 km W of Willowmavin site L). Oxygen consumption was measured by using compensating respirometers of the design of Davies (1966), with minor modifications (Mac Nally 1981a). For a given determination, the respirometer was immersed in a constant-temperature water-bath for 90 min prior to measurement to allow thermal equilibration. At the completion of the experiment, animals were blotted dry, and then weighed to the nearest 0.1 mg. They were then sacrificed, and dried for 6 wk at 55°C to obtain dry masses to the nearest 0.1 mg.

Measurements were regularised to standard temperature and pressure. Results should be considered to be routine metabolic rates (Fry 1957). The values are expressed as $\mu\text{l O}_2\text{h}^{-1}\text{g}[\text{dry}]^{-1}\text{STP}$, and were converted into energy units by using the oxycaloric conversion factor of 19.8 J ml O_2^{-1} (Elliot & Davison 1975). Measurements were made between 1200 h and 1800 h Eastern Australian Time during the synchronous periods of breeding in 1979 and 1980.

Time and energy budgets of behaviour: Time budgets of these species during reproductive activity are simplified by the fact that there are only two significant components to the behavioural repertoire: (1) production of vocalisations; and, (2) silent periods (see Mac Nally 1984a). Routines of measurement of schedules of calling consisted of recording the vocal activity of individual males over 10 min intervals of time. A variety of environmental parameters were measured to assess their influence on vocal activity (see Mac Nally 1984a). Of course, the schedules referred to activity of single males, so it was deemed necessary to standardise results to produce average schedules within choruses. Otherwise, there would be a tendency to overestimate call production if only, say, 70% of males were calling. The densities of males as determined above allowed estimates of the proportion of calling males at any one time. Standardised information then could be calculated. Calling schedules were quantified for most hours of the day and night so that daily schedules could be generated by the integration of these results (see Mac Nally 1984a). These results were translated into units of energy by using the method described in Mac Nally (1984a).

SOURCES OF ENERGY

Energy stores: Breeding males of both species were collected every 2-3 wk from Willowmavin F&M. Collections were made throughout the breeding seasons of 1977 and 1980. Fat-bodies and livers were removed by dissection, and these and the soma were weighed immediately, and again after having been dried for 4 wk or more at 55°C. Testes were also removed, but their small mass was of little consequence in relation to energy dynamics (Mae Nally 1981b).

A selection was made of samples from dates spanning the breeding seasons of both species in 1978 and 1979. The soma of all males in a given sample were ground together into a fine powder for use in standard calomet-

ric (Phillipson 1964) and ash-content (Reiners & Reiners 1972) determinations. An energy equivalent of 39 J=1 mg dry fat (Petruzewicz & Maefadyen 1970) was used. The livers of all males of a given species were pooled for the 1980 collections, and calorimetric and ash-content determinations again were undertaken.

Time-dependent patterns of change were derived for: somatic; hepatic; and, fat-body energy. These trends were used to establish the profiles of energy depletion throughout the breeding seasons of each species over the four years. Time-dependent changes in dry mass of soma were used in conjunction with data for metabolic rates to estimate the metabolic expenditures of males as the breeding seasons progressed.

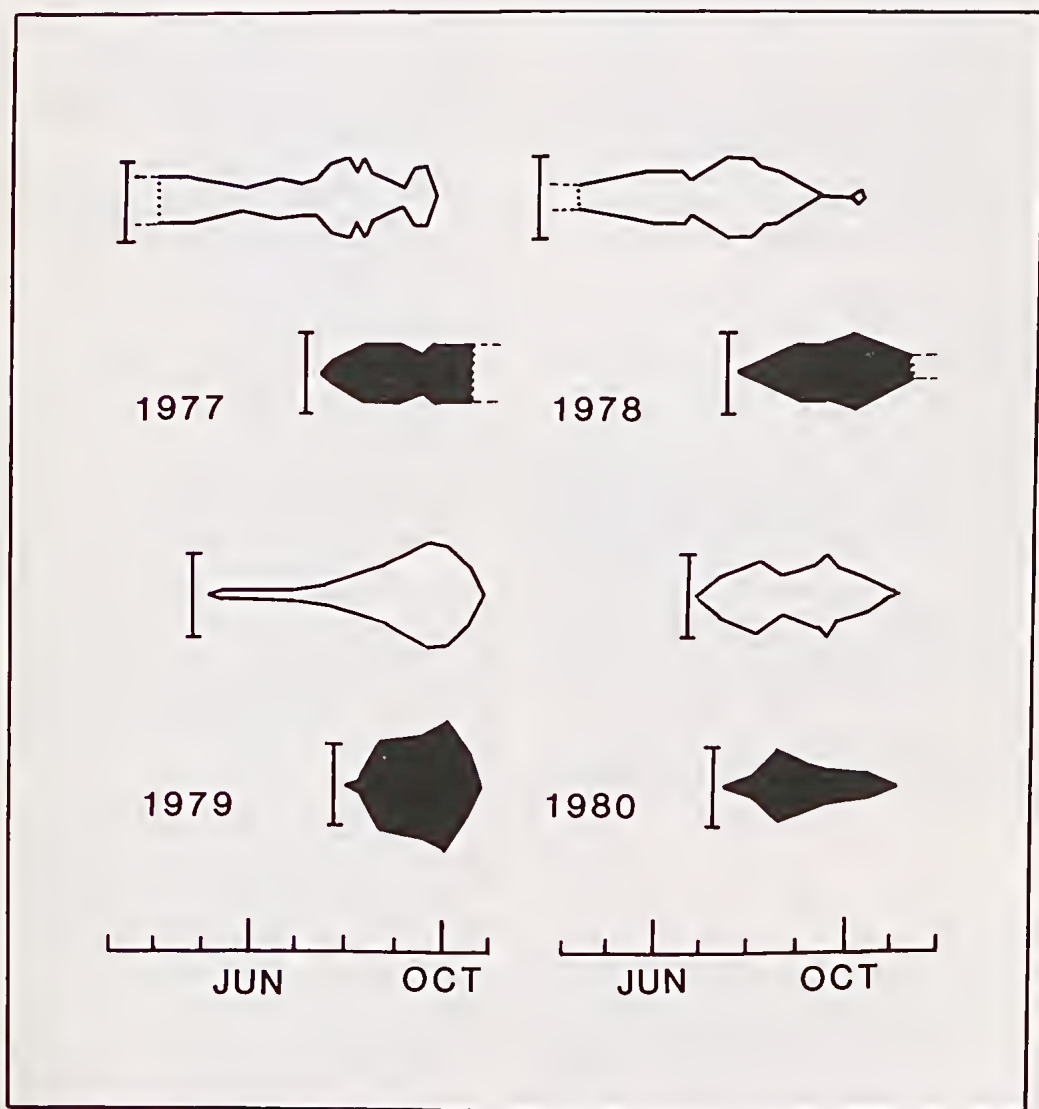


Fig. 1—Densities of breeding males (including satellites) throughout the breeding seasons of 1977 to 1980. Data are for *R. signifera* (open charts) and for *R. parinsignifera* (black charts). Bars associated with each chart equal 10 male m^{-2} . Dashed lines at ends of some charts indicate that individuals were present and active, but data were not collected in the manner described in the text.

TABLE 1

SUMMARY OF RESPIROMETRIC DATA FOR MALES OF *R. signifera* AND OF *R. parinsignifera* IN 1979 AND 1980. Metabolic rates are expressed in four units: $\mu\text{l O}_2\text{h}^{-1}\text{g}[\text{wet}]^{-1}$ STP; $\mu\text{l O}_2\text{h}^{-1}\text{g}[\text{dry}]^{-1}$ STP; J h^{-1} ; and, $\text{J h}^{-1}\text{g}[\text{dry}]^{-1}$. Data are $\bar{x} \pm \text{S.E.}$

Species and Temperature ($^{\circ}\text{C}$)	Number	Oxygen consumption		Energy equivalent	
		Wet	Dry	Wet	Dry
<i>R. signifera</i>					
5	18	60 \pm 5	249 \pm 21	1.2 \pm 0.1	4.9 \pm 0.4
10	12	86 \pm 4	325 \pm 15	1.7 \pm 0.1	6.4 \pm 0.3
15	12	169 \pm 12	629 \pm 45	3.3 \pm 0.2	12.5 \pm 0.9
<i>R. parinsignifera</i>					
5	18	61 \pm 4	252 \pm 17	1.2 \pm 0.1	5.0 \pm 0.3
10	12	84 \pm 8	328 \pm 31	1.7 \pm 0.2	6.5 \pm 0.6
15	12	163 \pm 9	646 \pm 36	3.2 \pm 0.2	12.8 \pm 0.7

RATES OF FEEDING

Stomach contents of males that were collected at Willowmavin F&M (see above) were placed onto small dishes and dried for 4-6 wk at 60°C . These amounts of food represent minimum daily rates of ingestion because males are liable to be feeding continuously throughout the day. Data were collected for the breeding seasons of 1977 to 1980.

FOOD AVAILABILITY

Absolute availability of prey was measured during the breeding season of 1981. Three replicate samples of sods of earth and associated vegetation from pond margins were collected from Willowmavin F&M every 3-4 wk. Sods measured $15 \times 15 \times 2$ cm. Invertebrates were extracted by using Berlese-Tullgren funnels (see Kevan 1962, Murphy 1962). The methods that were adopted assured the best overall retrieval of soil and litter invertebrates (Edwards & Fletcher 1971). The occurrence of more highly vagile taxa (e.g. adult dipterans) was monitored by using commercially-available flypapers, but very few prey taxa were captured by this method (1 per $80 \text{ cm}^2\text{d}^{-1}$). Therefore, no further reference is made to this source of information.

Where necessary, probability levels are designated by the conventional asterisk method: * $P < .05$; ** $P < 0.01$; and *** $P < .001$.

RESULTS

SPATIAL DYNAMICS

Males of both species form linear choruses along margins of ponds. However, more than 70% of males are located on land within 10 cm of the land-water interface (Mac Nally 1984c), so that the effective area of occupation is a strip 10 cm wide along pond margins. This means that 10 m of such a strip effectively constitutes 1 m^2 ; this conversion value allows areal estimates to be made for comparative purposes.

Densities of both species are shown for each of the four years in Fig. 1. There was autumnal drought in 1979

and 1980, which led to the concentration of breeding of both species into late winter and spring (Fig. 1). In the more normal rainfall years, 1977 and 1978, temporal overlap was much reduced (Fig. 1).

The average spatial density calculated over entire breeding seasons usually was about 5.0 males m^{-2} (Table 3). The sole exception was the unusually high density of males of *R. parinsignifera* in 1979, which was about twice as great (9.8 males m^{-2} ; Table 3).

EXPENDITURE OF ENERGY

Resting metabolism: There was no significant dependence of metabolic rates on year of measurement ($F_{1,60} = 0.62$), nor did the species differ ($F_{1,60} = 0.64$). Metabolic rates for each species for temperatures of 5, 10 and 15°C are listed in Table 1.

The estimation of daily costs of maintenance metabolism is much simplified by the fact that temperatures at the locations of males are highly concentrated around 10°C , irrespective of season (Table 2). Despite wide fluctuations recorded at representative weather stations, the temperature regime in a microgeographic sense is remarkably stable (Table 2). Therefore the costs of maintenance metabolism are considered to be dependent only upon changes in somatic mass as the season progresses (see below).

Costs of vocalisation and chorus participation: The methods by which these costs are estimated are described fully in another report (Mac Nally 1984a). Basically, they refer to the *additional* metabolic load during periods when males produce vocalisations (vocalisation load), or the *added* costs to non-vocalising males that are in the midst of active choruses (stimulation load). The factorial increases over resting metabolism are values derived from studies by Bucher *et al* (1982) and S. B. Chaplin and H. C. Gerhardt (pers. commun.) (but see Taigen & Wells 1985). The factorial values are: 4 (vocalisation load) and 1.5 (stimulation load). Stimulation load is subsumed into vocalisation load for periods during which males produce calls. For males of average size, representative values of daily metabolic costs are: (1) 23 J d^{-1} (maintenance); (2) 31 J d^{-1} (vocalisation); and, (3) 15 J d^{-1} (stimulation).

ENERGETICS AND FOOD LIMITATION IN *RANIDELLA*

TABLE 2

SUMMARY OF TEMPERATURE (°C) STATISTICS DURING THE BREEDING SEASON OF *R. signifera* AND *R. parinsignifera*. I present mean wet-bulb air-temperatures from four representative weather stations^a, and dry- or wet-bulb air-temperatures derived from the calling schedules, chorus mappings, or measurements made during the daytime at typical calling stations.

Time or category	Month							
	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov
0900	10.9 ^b	7.7	5.5	4.9	6.6	7.8	10.4	11.8
1500	13.5	10.4	8.9	7.8	8.9	9.8	12.3	14.0
Daily maximum	14.9	10.5	9.9	8.9	10.5	11.5	14.2	14.8
Daily minimum	6.4	3.8	2.0	1.4	3.2	3.4	5.1	7.1

Category	Month(s)	Time(s)	Dry/Wet bulb	$\bar{x} \pm S.D. (n)$
<i>R. signifera</i> schedules	Jul-Oct	all hours	wet	9.5 ± 2.3(124)
<i>R. signifera</i> mappings	Apr-Oct	1800-2200	dry	9.5 ± 3.3(159)
<i>R. parinsignifera</i> schedules	Aug-Oct	all hours	wet	9.9 ± 2.6(118)
<i>R. parinsignifera</i> mappings	Aug-Oct	1800-2200	dry	11.8 ± 3.1(94)
Diurnal measurements	Jun-Oct	1045-1800	dry	9.4 ± 1.7(48)

^a: Seymour (37°0'S, 145°9'E; 142 m elevation);
 Malmsbury (37°12'S, 144°24'E; 472 m);
 Kyncton (37°15'S, 144°27'E; 519 m);
 Mangalore (36°53' S, 145°11'E; 140 m).

^b: The 95% confidence interval of any one mean is $\pm 1.3^{\circ}\text{C}$ (viz., $\pm t_{.05,126} \sqrt{(MS[\text{within}]/4)}$; where there are 32 sets of 4 temperatures for each month for each category, and the variance of the 32 groups are homogeneous).

TABLE 3

ESTIMATES OF AVERAGE DAILY ENERGY EXPENDITURE, DEPLETION OF SOMATIC ENERGY RESERVES, AND CONSUMPTION OF FOOD BY BREEDING MALES OF *R. signifera* AND *R. parinsignifera* ALONG MARGINS OF PONDS. Duration of breeding seasons and mean spatial densities of males are listed.

	<i>R. signifera</i>				<i>R. parinsignifera</i>			
	1977(a)	1978(a)	1979	1980	1977(a)	1978(a)	1979	1980
Duration of breeding(d)	151	179	166	125	92	106	81	101
Mean density (males m ⁻²)(b)	4.6	4.9	5.1	5.6	5.5	5.3	9.8	4.0
Maintenance metabolism (J m ⁻² d ⁻¹)	137	134	148	149	143	130	269	107
Metabolic costs of reproductive behaviour (J m ⁻² d ⁻¹)	228	235	252	268	257	246	472	190
Total metabolism (J m ⁻² d ⁻¹)	365	369	400	417	400	376	741	297
Depletion of energy stores (J m ⁻² d ⁻¹)	40	47	75	78	64	100	296	68
Minimum consumption of food (mg[dry]m ⁻² d ⁻¹)	3.3	4.7	9.4	7.7	5.4	9.7	15.0	4.9
(J m ⁻² d ⁻¹)	75	107	213	175	123	220	341	111

(a) Minimum estimate because data were not collected for some parts of the breeding seasons.

(b) Equivalent to males per 10 m of pond margin.

TABLE 4
ESTIMATES OF ANNUAL EXPENDITURE OF ENERGY, DEPLETION OF SOMATIC RESERVES, AND MINIMUM CONSUMPTION OF FOOD BY BREEDING MALES OF *R. signifera* AND *R. parinsignifera* ALONG POND MARGINS.

Quantity	<i>R. signifera</i>				<i>R. parinsignifera</i>			
	1977(a)	1978(a)	1979	1980	1977(a)	1978(a)	1979	1980
Maintenance metabolism (kJ m ⁻² d ⁻¹)	20.6	24.0	24.5	18.6	13.2	13.8	21.8	10.8
Metabolic cost of reproductive behaviour (kJ m ⁻² d ⁻¹)	34.4	42.0	41.7	33.6	23.7	26.1	38.2	19.1
Total metabolism (kJ m ⁻² d ⁻¹)	55.0	66.0	66.2	52.2	36.9	39.9	60.0	29.9
Depletion of energy stores (kJ m ⁻² d ⁻¹)	6.1	8.3	12.5	9.8	5.9	10.6	24.0	6.9
Minimum consumption of food (mg[dry]m ⁻² yr ⁻¹)	510	840	1570	1030	510	990	1210	500
(kJ m ⁻² yr ⁻¹)	11.6	19.1	35.6	23.4	11.6	22.5	27.5	11.4

(a) Minimum annual estimate because data were not collected for some parts of the breeding seasons.

Throughout the remainder of this paper, costs of vocalisation and stimulation are treated under the one category of reproductive behaviour.

Population energetics—daily expenditure: Mean expenditure of breeding males per day varied relatively little between years in choruses of *R. signifera* (Table 3). The population-wide cost of maintenance metabolism was about 140 J m⁻²d⁻¹, whereas the estimated added expenditure (*viz.*, over and above maintenance) due to reproductive behaviour ranged from 228–268 J m⁻²d⁻¹. Total population metabolism was in the range of 365–417 J m⁻²d⁻¹ (Table 3). Estimates for choruses of *R. parinsignifera* were more variable, owing to the uncommonly dense aggregations that persisted throughout 1979 (Table 3). The population expenditure on maintenance (107–269 J m⁻²d⁻¹), reproductive behaviour (190–472 J m⁻²d⁻¹), and total (297–741 J m⁻²d⁻¹) metabolism showed ranges of more than two-fold variation commensurate with the range in average daily density (Table 3).

Population energetics—annual expenditure: Annual expenditure by breeding males of *R. signifera* was relatively consistent from year to year, notwithstanding the effects of drought in 1979 and 1980 in concentrating reproductive activity into shorter time-spans (Table 4). Annual population expenditures were: (1) maintenance (18.6 to 24.5 kJ m⁻²yr⁻¹); (2) reproductive behaviour (33.6 to 42.0 kJ m⁻²yr⁻¹); and, (3) total metabolism (52.2 to 66.2 kJ m⁻²yr⁻¹). The greater average density of males of *R. parinsignifera* in 1979 was reflected in annual population metabolic costs that were similar to those of *R. signifera* despite a much shorter breeding season (Table 4). In other years, the figures for populations of *R. parinsignifera* were somewhat less than those of their congeners (50% to 63%) (Table 4).

SOURCES OF ENERGY

Energy depletion profiles: Regression lines that depict the changes in total energy of soma are shown in Fig. 2. Relationships for males of both species for each of the four

years are illustrated. Some sets of data are best represented by curvilinear polynomial relationships (Fig. 2). Also shown are the mean surpluses of somatic energy of average males of *R. parinsignifera* over average males of *R. signifera* (Fig. 2) according to the equation:

$$\bar{E}_s = \left[\int_i^f [P(t) - S(t)] dt \right] / \left[\int_i^f dt \right], \quad (1)$$

where: P(t) and S(t) represent the time-dependent functions of total somatic energy of *R. parinsignifera* and *R. signifera* respectively; and, i and f define the start and finish of synchronous occurrence at breeding sites. Evaluation of equation (1) for each of the four years showed that males of *R. parinsignifera* enjoyed an energetic superiority of 880 J d⁻¹ and 424 J d⁻¹ in 1978 and 1977, but much more equal stores were seen in the drought years of 1979 and 1980 (54 J d⁻¹ and -70 J d⁻¹ respectively). As males expend, on average, 69 J d⁻¹, it is clear that the effect of drought is to reduce superiority of energy stores of *R. parinsignifera* over their congeners from about 6–13 d in normal years to less than 1 d in drought-affected years.

The daily depletion of energy stores (*i.e.* negative production excluding losses due to mortality) in populations varies between 40 and 78 J m⁻² d⁻¹ in *R. signifera* and between 64 and 296 J m⁻² d⁻¹ in *R. parinsignifera* (Table 3). The relatively great figure of 296 J m⁻² d⁻¹ calculated for *R. parinsignifera* in 1979 does not appear to be unrealistic given that there were large densities of males (9.8 males m⁻²) and a steep gradient on energy depletion profiles as well (see Fig. 2). However, it seems that daily depletion rates of about 70 J m⁻² d⁻¹ would be more characteristic of these species (Table 3).

Estimates of annual depletion of stores of energy are listed in Table 4. The values range between 6.1 and 12.5 kJ m⁻² yr⁻¹ in *R. signifera*, and between 5.9 and 24.0 kJ m⁻² yr⁻¹ in *R. parinsignifera*. Again the high average density of the latter species in 1979 was the cause of the relatively large value of 24.0 kJ m⁻² yr⁻¹. One would characterise annual depletions in populations of these species as something of the order of 8 to 10 kJ m⁻² yr⁻¹ (Table 4).

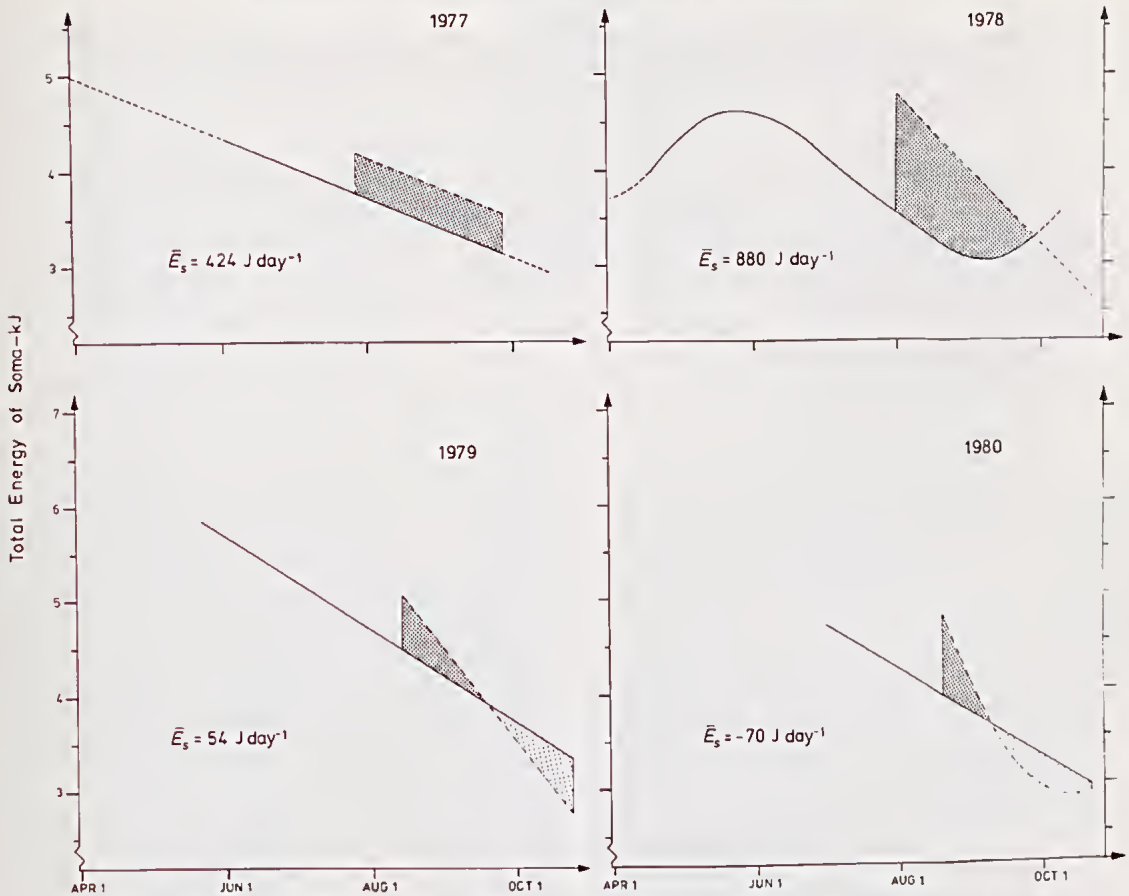


Fig. 2—Regression lines of best-fit of total energy of soma plotted against time for both species of *Ranidella* for four years. Solid lines (dashed ends in 1977, 1978) represent data for *R. signifera*, whereas dash-dot lines (---) represent information for *R. parinsignifera*. Relative levels of total somatic energy are shown: heavy stippling—*R. parinsignifera* superior to *R. signifera*; light stippling—*R. signifera* superior to *R. parinsignifera*. The average daily excess of total somatic energy of males of *R. parinsignifera* over their congeners is also supplied (\bar{E}_s , see text). Correlation coefficients: *R. signifera*, 1977 ($r=0.49^{***}$, $n=68$), 1978 ($r=0.69^{***}$, $n=90$), 1979 ($r=0.59^{***}$, $n=65$), 1980 ($r=0.65^{***}$, $n=57$); *R. parinsignifera*, 1977 ($r=0.28$ n.s., $n=39$), 1978 ($r=0.86^{***}$, $n=47$), 1979 ($r=0.74^{***}$, $n=22$), 1980 ($r=0.74^{***}$, $n=38$).

An estimate of the total loss of energy stores in populations of breeding males of these species must account for mortality that occurs during the breeding season. A mortality rate of 25% has been recorded at a breeding site near Canberra, Australia (Humphries 1979). I estimate by using this figure that total negative production incurred by breeding males during a breeding season would be from 9.6 to 16.7 $\text{kJ m}^{-2} \text{yr}^{-1}$ in *R. signifera*, and from 9.9 to 31.1 $\text{kJ m}^{-2} \text{yr}^{-1}$ in *R. parinsignifera*. A representative figure for populations would be of the order of 12 to 14 $\text{kJ m}^{-2} \text{yr}^{-1}$.

Consumption of food at breeding locations: Minimum consumption of food by breeding males is represented in units of dry mass, and also of energy by assuming a conversion factor of 22.7 $\text{J mg}[\text{dry}]^{-1}$ (Griffiths 1977) (see Tables 3, 4). Daily estimates range from 75 to 213 $\text{J m}^{-2} \text{d}^{-1}$ in *R. signifera*, and from 111 to 341 $\text{J m}^{-2} \text{d}^{-1}$ in *R. parinsignifera* (Table 4). In both daily and annual estimates for both species, there is too much variation to specify a characteristic value for populations of breeding males.

ENERGY REQUIREMENTS AND AVAILABILITY

Mean daily costs of maintenance and of reproductive activity are listed in Table 3. We are now in a position to compare these requirements with measurements of energy availability to finance these costs. The two possible sources of energy, imported somatic stores and food, have been evaluated above. However, the values obtained for these sources are subject to constraints on transfer efficiency. Specifically, only 50% of energy stores can be used after mobilisation (White *et al.* 1964), and efficiency of assimilation by adult anuran amphibians is of the order of 75% (Smith 1976).

I define *energy shortfall* to be the difference between energy requirements and usable energy derived from energy stores. The shortfall can only be bridged by feeding.

Use of energy stores provides relatively little of the energy needed to finance metabolic expenditures. In *R. signifera*, only 5.5 to 9.5% of necessary energy can be met from this source. The figures are higher in *R. parinsig-*

TABLE 5

SUMMARY OF ENERGY ACQUISITION AND EXPENDITURE IN POPULATIONS OF BREEDING MALES OF *R. signifera* AND *R. parinsignifera*. These data refer to average daily conditions. Energy acquisition values have been modified to incorporate efficiency coefficients, so that the values stated here are usable energy estimates. All units are $J m^{-2}d^{-1}$.

Quantity	<i>R. signifera</i>				<i>R. parinsignifera</i>			
	1977(a)	1978(a)	1979	1980	1977(a)	1978(a)	1979	1980
Metabolic expenditure	365	369	400	417	400	376	741	297
Energy shortfall	345	345	362	378	368	326	543	263
%: Minimum consumption over shortfall	16.2	23.2	44.2	34.7	25.0	50.6	47.1	31.6
%: Shortfall over mean availability of standing crop	10.1	10.1	10.6	11.1	10.8	9.6	16.0	7.7

(a) Minimum estimates because data were not collected for some parts of the breeding seasons.

nifera (8.0 to 26.7%) by virtue of the fact that males of this species deplete about the same amount of stores (approx. $2200 J yr^{-1}$, Mae Nally 1981b) in considerably less time (see Table 3). Nevertheless, feeding must provide the majority of the energy to satisfy the metabolic requirements.

The amounts of usable energy equivalent to rates of minimum consumption of food do not bridge the energy shortfall (Table 5). The percentage of minimum consumption to shortfall ranges from 16.2 to 44.2% in *R. signifera*, and from 25.0 to 50.6% in *R. parinsignifera* (Table 5). A reasonable characteristic percentage would be 35–40% in these species. This means that males must consume during the day between two and three times the amount of food that is present in their stomachs in early evening.

Mean absolute availability of the invertebrate taxa that are consumed by males of these species was quite consistent, being of the order of $200 mg [dry] m^{-2}$ from July to October (see also Mae Nally 1983b). Of course, this amount corresponds to only 75% as much in usable terms (given efficiency of assimilation), so that absolute availability would be $150 mg [dry] m^{-2}$ or $3.4 kJ m^{-2}$ standing crop.

Approximately 10% of absolute availability is required to overcome the daily energy shortfall in both species (Table 5). One concludes from these figures that the combined daily impact of feeding by breeding males in syntopic conditions is about 20% of the standing crop. To sustain such an impact would require a rather unlikely level of 20% daily production of those prey taxa that were found to occur in the diets of males of *R. signifera* and *R. parinsignifera*.

DISCUSSION

COMPARATIVE POPULATION ENERGETICS OF TERRESTRIAL VERTEBRATES

Details of components of population energetics of representatives of each of the four classes of terrestrial vertebrates are listed in Table 6. An examination of these figures suggests two main conclusions. First, populations of poikilothermic vertebrates can rival avian and mammalian populations in terms of food consumption and respiration. To do so, however, their populations must be

either highly concentrated, like aggregations of breeding *Ranidella*, or else such populations must be of relatively great general abundances (saurofauna of Bennett & Gorman 1979). Second, if the populations of poikilotherms are not concentrated, or have standing crops of about the same magnitude as avian or mammalian populations, then both the metabolic expenditure and impact on prey (or plants) is of little consequence in relation to populations of homeotherms (compare data for *Uta* and salamanders with birds and mammals). One can generalise these comments and conclude, as others have done (Alexander & Whitford 1968, Burton & Likens 1975), that poikilothermic vertebrates have little impact on broad-scale energy transformations in ecosystems relative to homeothermic vertebrates.

Burton and Likens (1975) observed that the ratios of production to respiration in populations of salamanders was of the order of sixty times greater than that of sympatric avian populations. I believe that the data provided in the present paper indicate that the population energetics of salamanders are not characteristic of amphibians as a whole. The caudate amphibians, of which salamanders are representatives, probably differ much from anuran amphibians by virtue of the great investment that male anurans make in reproductive displays (Ryan *et al.* 1983, Mae Nally 1984a, Taigen & Wells 1985). This leads to greatly elevated metabolic expenditure, and also, much negative production as breeding males dissipate energy stores as the season progresses (Smith 1976, Mae Nally 1981b, present paper). A brief comparison demonstrates the impact on energetics of vocal activity. Burton and Likens (1975) estimate that the total production of salamanders is of the order of $20 kJ ha^{-1} yr^{-1}$, yet the combined dissipation of energy by breeding males of *Ranidella* is over 10^4 as much, $260 MJ ha^{-1} yr^{-1}$. Admittedly, much of the disparity between these figures is derived from the relatively high concentration of males of *Ranidella* at breeding sites, but nevertheless, this amount of loss must be restored before any positive production can be made. The figures for respiration confirm that the high productivity:respiration ratios reported by Burton and Likens (1975) are unlikely in anurans. The estimated metabolism of salamanders at Hubbard Brook is about $12.5 MJ ha^{-1} yr^{-1}$, compared with the figures of males of *Ranidella*

TABLE 6
 REPRESENTATIVE ESTIMATES OF STANDING CROP (kg ha⁻¹), CONSUMPTION OF FOOD (MJ ha⁻¹yr⁻¹) AND RESPIRATION (MJ ha⁻¹yr⁻¹) IN POPULATIONS OF TERRESTRIAL VERTEBRATES.

Faunal type	Standing Crop	Consumption	Respiration	Authority
Avifauna	0.65	309.0	214.1	Holmes & Sturgess 1973, 1975
Avifaunas	0.22-0.53	371.2-890.7	438.9-868.6	Wiens & Nussbaum 1975
Avifaunas	—	45.4-83.8	33.1-61.5	Wiens 1977
Avifauna	0.11	—	51.7	Holmes <i>et al.</i> 1979
Small mammals	1.13	564.0	419.2	Chew & Chew 1970
Small mammals	1.02	747.3	591.6	Grodzinski 1971
Small mammals	0.08-0.81	71.6-825.1	47.7-530.1	French <i>et al.</i> 1976
<i>Uta stansburiana</i>	0.18	30.1	10.0	Alexander & Whitford 1968
Lizards	10.0	508.5	—	Darevskij & Terentev 1967
Snakes	0.8	29.2	—	Darevskij & Terentev 1967
<i>Sauromalus obesus</i>	1.67	37.7	18.8	Nagy & Shoemaker 1975
Saurofauna	23.1	2095.1	1313.6	Bennett & Gorman 1979
Salamanders	1.78	29.4	12.5	Burton & Likens 1975
Terrestrial anurans	5.6	70.3	—	Darevskij & Terentev 1967
Aquatic anurans	67.6	780.4	—	Darevskij & Terentev 1967
Syntopic <i>Ranidella</i>	55	±233	508	Present study

508 MJ ha⁻¹ yr⁻¹, of which about two-thirds is due to costs of reproductive activity (Table 6). I believe that the prevalence of vocalisation as a reproductive activity of male anuran amphibians (see Wells 1977) ensures that the ratios of production to respiration in this order will be intermediate between values cited for caudate amphibians, and those reported for homeothermic vertebrates. Clearly, more detailed studies of population dynamics and energy expenditure in anuran amphibians are required to examine the hypothesis just described.

Recently, more estimates of the metabolic load of vocalisation have become available (Taigen & Wells 1985). These studies suggest that the factorial increase during call-production may be two to three times as great as the value used here. If the factorial increase in *Ranidella* indeed was of the order of 10 to 15 fold, then the disparity in production:respiration ratios between caudate and anuran amphibians would be even more pronounced. In following sections of this paper, I point out that food availability seems unlikely to satisfy demands under the assumption of a 4 to 5-fold factorial increase. Therefore, any revision to higher loads would only support the notion of limited energy availability with respect to requirements. This should be borne in mind when considering these sections of the discussion.

SOURCES OF ENERGY

A major observation is that energy reserves contribute relatively little to the financing of energy expenditure of breeding males. That is, less than 10% of the expenditure of a male of *R. signifera* can be drawn from energy reserves, and less than 25% in *R. parinsignifera*. Congdon *et al.* (1979) deduced that overwintering lizards could gain less than 50% of their requirements from energy reserves, but if one includes an efficiency of conversion factor of about 50%, the lizards would need to accrue more than 75% of their needs from feeding. Two things are apparent from these observations. First, somatic energy reserves

are unlikely to be able to meet the energy requirements of breeding (or indeed hibernating) reptiles and amphibians. This implies that food is likely to be an important resource in breeding aggregations, at least for species with prolonged breeding seasons (see Wells 1977). Second, dissipation of energy reserves is an unreliable indicator of the actual magnitude of energy expenditure of individuals during breeding because of feeding at breeding sites.

The amounts of food that were recovered from the stomachs of males can account for only 40% of the energy shortfall that they experience daily. This value indicated that males must consume at least 2-3 times as much during a day to allow them to continue to breed. Johnson and Christiansen (1976) performed feeding experiments of individuals of *Acris crepitans* to determine the rates at which food passed through the digestive tract. This species, which is ecologically similar to the species of *Ranidella* (although somewhat larger, ca 1.2 g compared to 0.6 g), has digestion rates of about 8 h, which is in good agreement with the length of time that would be necessary to digest the amount of food required by breeding males of *Ranidella*. One concludes that it is possible for males of these species of *Ranidella* to digest and assimilate enough food to cover the estimated expenditures of energy.

COMPARISONS OF INDIVIDUAL REPRODUCTIVE EFFORTS

Variables necessary to define reproductive energetics of individuals of small species of poikilothermic vertebrates are listed in Table 7. Ryan *et al.* (1983) have supplied a similar table, but more information and modified analyses are presented in Table 7. An immediate observation is that daily mass-specific expenditure on reproduction (J g⁻¹ d⁻¹) varies relatively little despite wide variation in length of breeding season, except for females of *Uta stansburiana*, which expend of the order of two to four times as much as any other group (Table 7).

Ryan *et al.* (1983) reported that the sexes of a neotropical anuran, *Physalaemus pustulosus*, differ by more than

TABLE 7
COMPARISONS OF THE REPRODUCTIVE EXPENDITURES OF MALES AND FEMALES OF SMALL REPTILES AND AMPHIBIANS

Sex	Species	Mass(g)	Duration of breeding(d)	Expenditure(kJ)	kJg ⁻¹	Jg ⁻¹ d ⁻¹
♂	<i>Uta stansburiana</i> (a)	3.3	117	21.5	6.5	56
1+ ♀	<i>Uta stansburiana</i>	2.3	117	44.8	19.5	166
2+ ♀	<i>Uta stansburiana</i>	2.7	117	45.4	16.8	144
♀	<i>Desmognathus ochropaeus</i> (b)	1.0	c.150	5.1	5.1	34
♀	<i>Physalaemus pustulosus</i> (c)	1.8	259	41.0	22.8	88
♂	<i>P. pustulosus</i>	1.7	44	3.3	1.9	44
♂	<i>Ranidella</i> (d)	0.6	80	3.7	6.2	77
♀	<i>Ranidella</i> (d)	0.9	?	>2.2	>2.4	?

(a) lizard (Nagy 1982);

(b) salamander (Fitzpatrick 1973);

(c) anuran (Ryan *et al.* 1983);

(d) anuran (present study, Mac Nally 1982, 1984a).

an order of magnitude in relation to reproductive expenditure. However, two of their critical data may be erroneous, and may have contributed to the large imbalance that they report. First, they calculated total seasonal expenditure of males on the basis of a 259 d breeding season, yet the average duration of reproductive activity of any individual male was of the order of 40 d or so. Second, they assumed that females of this species produce as many as 10 clutches in the 259 d span of time, despite the absence of concrete field data with which to substantiate this estimate. I make these points because I believe that the results of Ryan *et al.* (1983) may lead to a widespread belief that female anurans always expend much more energy on reproduction than conspecific males, and thereby conform to patterns believed to occur in homeothermic vertebrates (e.g. Trivers 1972). Results that are presented for the two species of *Ranidella* contradict the conclusions of Ryan *et al.* (1983) (see Table 7). There seems to be relatively little difference between the sexes in *Ranidella* in terms of reproductive expenditure (Mac Nally 1984a). There are conclusive field data that show that females of *R. signifera* and *R. parinsignifera* rarely, if ever, produce more than a single clutch per year, despite breeding seasons of about 130 d (Humphries 1979). Moreover, the daily, mass-specific expenditure of males of *Ranidella* is comparable to that of females of *P. pustulosus*, and about twice that of females of *Desmognathus ochropaeus* (Table 7).

It seems possible that any disparities of reproductive expenditure of the sexes of anurans may be related to the nature of the breeding system that is involved (see Wells 1977). The reasoning behind such an assertion is this. Females are able to accumulate energy for vitellogenesis over a long period of time preceding the actual breeding season; in fact, females of many species arrive at breeding sites with mature complements of ova and deposition quickly occurs. In contrast, males are unable to contribute to their reproductive expenditure in this way, and costs are related to duration of reproductive activity. Clearly, in explosive breeding systems (*sensu* Wells 1977), the time available for males to engage in reproductive activity is

short (say 2 wk), whereas the female investment may commence many months prior to breeding. An imbalance is to be expected on these grounds. In prolonged breeders, of which the two species of *Ranidella* are representatives, the time available for males to expend energy is much extended, thereby leading to an elevated likelihood of more equal expenditures on reproduction between the sexes. Why then, is the more prolonged breeding season of *P. pustulosus* associated with an extreme imbalance? The most likely reason is that the sexes of this species differ in the *effective* lengths of breeding seasons (see Table 7). Individual males have breeding seasons of effective duration of just 7 d (Ryan *et al.* 1983), characteristic of explosive breeders, but individual females continue on for much longer periods, that are more characteristic of seasons of prolonged breeders. It seems that heavy, sex-specific, acoustic-related predation by bats upon males leads to such a disparity in duration of breeding by individuals of the sexes of *P. pustulosus* (see Ryan *et al.* 1981, Tuttle & Ryan 1981).

FOOD LIMITATION?

The impact of the feeding of males of *R. signifera* and *R. parinsignifera* is likely to be great because of the interplay of a number of behavioural characteristics of these species. First, males are concentrated into narrow bands that surround ponds. Males are sedentary, not only during the day, but also throughout the breeding season (Mac Nally 1979, 1984a, c). Second, there is no trophic or micro-habitat segregation between the two species (Mac Nally 1983b, 1985). Third, the males do not seem to utilise the entire range of potential invertebrate prey taxa that occupy pond margins (Mac Nally 1983b). If they did so, there would be more than six times as much food available to them as there currently is (Mac Nally 1983b).

The daily requirements of sympatric populations of these species of *Ranidella* is at least 20% of the standing crops of utilised prey taxa. Of course, food limitation will be determined not by standing crop, but rather, by the production of the invertebrate prey taxa. No direct meas-

urements of productivity currently exist for the site under consideration, but much work has been done on the productivity of such invertebrate populations (e.g. Waters 1977, Banse & Mosher 1980). A reasonable ratio of production:biomass is about 4.5 (Waters 1977, Banse & Mosher 1980). Even a value of this order is insufficient to sustain the requirements of the anuran males. One should add a caveat here, that the prey availability was determined in the year following the four main years of study. Clearly, greater reliability would be attained if all aspects of the study could be conducted simultaneously. I do not believe that the results would be changed materially, because densities of males were similar in 1981 to those in 1977 and 1978 (unpublished observations).

The model of energy requirements and food availability that is presented here indicates that food is likely to be limited along pond margins. Are there any repercussions that have been observed in populations of these species? Clearly, there is no segregation of prey taxa, prey size-distribution or microhabitat (Mac Nally 1983b, 1985). There is variable temporal overlap (Fig. 1), and it is possible that the stored energy surplus (\bar{E}_s) enjoyed by males of *R. parinsignifera* over their congeners in 1977 and 1978 (Fig. 2) allowed them to continue breeding when their congeners did not in those years (Fig. 1, Mac Nally 1984b). It would seem to be advantageous to explore the question of food limitation by experimentally altering the densities of breeding males of these species of *Ranidella*. Until such experiments are undertaken, one cannot gauge whether the apparent shortages of food are translated into effects of densities of males of each species, and hence into temporal segregation.

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